Predation by the non-native fish *Gambusia holbrooki* on small *Litoria aurea* and *L. dentata* tadpoles

L. A. Morgan[1] and W. A. Buttemer[2]
[1]Environmental Science Unit, University of Wollongong, Wollongong, New South Wales 2522.
[2]Department of Biological Sciences, University of Wollongong, Wollongong, New South Wales 2522.

ABSTRACT

Gambusia holbrooki, the "Mosquito Fish" introduced to Australian waterways from North America to control mosquito larvae, is widely distributed and abundant in both disturbed and undisturbed aquatic environments. Because it has become established in areas where *Litoria aurea* was once abundant, there is some suspicion that *G. holbrooki's* non-specific predatory behaviour may be instrumental in the decline of *L. aurea*.

Laboratory and field experiments were conducted to assess the impact of *G. holbrooki* predation on *L. aurea* tadpole survivorship. Laboratory trials involved placing 30 *L. aurea* tadpoles per 46-litre aquarium in each of the following four treatments: control treatments (two aquaria with just tadpoles and two aquaria with tadpoles and the pondweed, *Egeria densa*) and two predator treatments (two aquaria with fish and tadpoles and two aquaria with tadpoles, fish and pondweed). A daily census of the tadpoles was taken over four days. Based on ANOVA of six aquaria for each treatment, *G. holbrooki* significantly reduced *L. aurea* survivorship, but pondweed had no significant effect until the final census. The same experimental procedures were used for *L. dentata*. Again, tadpole number was significantly lower in aquaria housing *G. holbrooki* than in those without these fish, and pondweed influenced *L. dentata's* survival only on the final 72-hour census.

Field experiments were conducted by placing 30 *L. aurea* tadpoles in 1.5 × 0.6 × 0.6 m screened cages which permitted water-flow but excluded predatory fish. A pair of cages (one with six *G. holbrooki* and one without) were placed in three separate ponds on two occasions. A daily tadpole census taken over four days revealed that tadpoles exposed to *G. holbrooki* had significantly higher daily mortality than tadpoles which were caged alone.

These results show conclusively that *G. holbrooki* is a predator of *L. aurea* and *L. dentata* tadpoles. Future management decisions regarding *L. aurea* populations should include a consideration of *G. holbrooki's* impact as well as methods for their removal from breeding sites.

INTRODUCTION

The evidence from many reports during the past 20 years has generated the widely held concern that amphibians (frogs, toads, salamanders and caecilians) are declining in both number and distribution throughout the world (Barinaga 1990; Blaustein and Wake 1990; Pechmann *et al.* 1991; Wake 1991; Hedges 1993; Pechmann and Wilbur 1994; Blaustein *et al.* 1994; Pounds and Crump 1994). Australian amphibians have proved no exception (Osborne 1990; Tyler 1991; Osborne 1992; Ferraro and Burgin 1993; Ingram and McDonald 1993; Gillespie *et al.* 1994; Richards *et al.* 1993; Tyler 1994).

Litoria aurea Lesson, a frog species once common to permanent water-bodies of south-eastern Australia, has undergone a decline in its distribution and abundance over the past 15 years (Osborne 1986; Mahony 1993; Daly 1995; Osborne *et al.* 1996). In New South Wales, it is recognized as a "threatened" species (Schedule 12, *NSW National Parks and Wildlife Service Act* 1). One of the factors thought to influence its decline is predation by the introduced fish, *Gambusia holbrooki* Girard (Mahony 1993; Daly 1995).

Gambusia are small freshwater fish, native to the southern United States of America and Central America. *G. holbrooki*, a sub-species of *G. affinis* was introduced world-wide to control mosquito larvae (Lloyd and Tomasov 1985). *G. holbrooki* was introduced to Australia for this purpose in 1925 (Myers 1965), and the species is presently widespread in inland and coastal drainage systems (McDowall 1980; Lloyd *et al.* 1981; Faragher and Harris 1994). Predation by a non-native fish species may reduce the larval, and in turn the adult population size of frogs (Semlitsch 1993), including *L. aurea*.

The extent of predation by *G. holbrooki* on *L. aurea* tadpoles was evaluated using both laboratory and field-based experiments. Established aquatic vegetation, particularly submerged plants are part of the habitat of permanent water-bodies. Such plants (e.g., *Egeria densa*) may provide an important refuge for tadpoles trying to escape predation. Consequently, the effect of aquatic vegetation with respect to tadpole survivorship was evaluated in the laboratory experiments.

To examine whether *L. aurea* is more susceptible than sympatric species not showing population declines, one laboratory trial examined survivorship of *L. dentata* in the presence of *G. holbrooki*.

MATERIALS AND METHODS

Species Collection and Maintenance

The collection of *L. aurea* tadpoles and all experiments involving them was approved by the NSW National Parks and Wildlife Service (scientific licence Class B 1291) and the University of Wollongong Animal Experimentation Ethics Committee (AE94/18). Experiments involving *L. dentata* were also approved by NSW National Parks and Wildlife Service.

L. aurea larvae were collected in December 1994 and January and February 1995 from the spawn of amplectant frogs from the Port Kembla and Rosebery, New South Wales breeding populations. *Litoria dentata* larvae were taken from the collected spawn of amplectant frogs from Helensburgh, New South Wales in December 1994. *G. holbrooki* were taken from the University of Wollongong Duck Pond for each experimental trial from January to March 1995.

Tadpoles were kept in containers of unfiltered pond water in a room maintained at 20°C and lit by ambient light. Space constraints meant that the number of tadpoles kept in each container varied from as many as 70 per 4 litres to 8 per 46 litre containers. To help alleviate these high density conditions and to maintain water quality the water was changed every three days.

Tadpoles were fed boiled lettuce supplemented by ground rat food pellets ("Chequerboard" brand, Allied Stockfeeds) and fish food flakes ("Aiwa" brand). Food was supplied when previous supplies had been eaten, usually every two to three days.

Experimental Design and Protocol

To evaluate the extent of predation by *G. holbrooki* on *L. aurea* and *L. dentata* tadpoles, a series of laboratory and field-based experiments were conducted. All of these used an initial predator-prey ratio of 1:5 after the methods of Travis *et al.* (1985) and Webb (1994). The predator treatment used six *G. holbrooki* and 30 tadpoles in each aquarium or cage. Control treatments used 30 tadpoles only.

The seven laboratory trials used a standard randomized complete block design where the four treatments have a 2 × 2 factorial structure. Each trial consisted of two control treatments (two aquaria with just tadpoles and two aquaria with tadpoles and the pondweed, *E. densa*) and two predator treatments (two aquaria with fish and tadpoles and two aquaria with tadpoles, fish and pondweed).

Eight white plastic bins, (600 × 360 × 380 mm) containing 46-litres of filtered pondwater were used as aquaria. Each aquaria contained a substrate filter, a 2 cm layer of coarse gravel and the aerator, a vertical tube. Four aquaria housed approximately 100 g (wet mass) of *E. densa* plants collected in January from the University of Wollongong Duck Pond. The aquaria were kept in a 20°C laboratory with a photoperiod of 12L:12D.

For a given trial tadpoles from either the Port Kembla or Rosebery population were selected. Body length measurements of tadpoles were taken before and after a trial, using a standard ruler to determine snout-vent length (SVL) and total body length (TL) to the nearest millimetre. The *L. aurea* and *L. dentata* tadpoles used were less than 8 mm in snout to vent length (Gosner pre-stage 25, Gosner 1960). For the second laboratory trial, 97 *L. aurea* tadpoles used in the second field trial were re-used due to a shortage of tadpole stock at that time. Every other trial used fresh tadpoles.

Freshly-caught *G. holbrooki* were sorted into each treatment by size. In each treatment within a trial, three fish larger than 25 mm (mean: 28 mm ± 1 s.e., $n = 168$) and three smaller than 25 mm (mean: 19 mm ± 1 s.e., $n = 168$) in TL were selected.

Both predator and prey were simultaneously introduced to the treatment environment during the light phase. Food for both animals (fish food flakes and prepared lettuce) were also added at the beginning of a trial and again every 24-hours during a trial.

The survival of tadpoles was recorded at 24-hour intervals by taking a census of each treatment environment. The number of tadpoles deceased, and alive, including those surviving fish attack/s were recorded. Body length measurements of dead tadpoles were not taken because their bodies had become flaccid. Dead tadpoles were returned to the aquaria with the remaining tadpoles.

To minimize experimental bias the treatment effect tested within each aquarium changed between trials (e.g., if an aquarium served as a control environment previously, then predatory fish were placed in this aquaria for the upcoming trial). *E. densa* plants were also exchanged between aquaria after each trial.

Two field trials were run using Port Kembla tadpoles at three pond sites. The selection of suitable waterbodies was dictated by the following criteria: permanency of water, lentic conditions, a near shore depth of approximately 30 cm maximum, the presence of *G. holbrooki*, and proximity to the other two sites. These ponds were: Pond 1, the University of Wollongong

Duck pond; Pond 2, the Bridge pond, University of Wollongong; and Pond 3, the largest pond at Wollongong Botanic Gardens.

Tadpoles were housed in predator-exclusion cages which were built using a 1.5 × 0.6 × 0.6 m timber frame covered on five sides with screen mesh (7 strands/cm, stapled to frame) after the methods of Sredl and Collins (1992). A mesh (1 strand/cm) lid was sewn to the screen mesh sides and rocks placed inside the cages anchored them on the substrate. Two semi-immersed cages were used per site. One cage contained 30 *L. aurea* tadpoles only and the other held both tadpoles and fish in the established 1:5 ratio.

In contrast to the laboratory trials, *G. holbrooki* were not provided with food. However, *L. aurea* were supplied with boiled lettuce at each 24-hour census.

Data Analysis

Cochran's test for homogeneity of variance was applied to raw and transformed data from the laboratory and field trials. A 2 × 2 fixed factorial analysis of variance (ANOVA) test, using arcsine transformed data was applied to census data derived from the laboratory trials, as well as for the single trial using *L. dentata*. Untransformed census data from the two field trials were analyzed using a one-way ANOVA.

RESULTS

Litoria aurea *Tadpoles*

During the fourth, fifth and sixth laboratory trials up to five aquaria were found to contain one or two damselfly larvae (Odonate: Zygoptera), an invertebrate predator. To maintain a within-trial balanced design with equal replication, all census data from affected aquaria and their treatment contrast were removed including other treatment pairs as required. Four trials with six replicates of each treatment remained for statistical analysis. These four trials as well as the two field trials used *L. aurea* tadpoles with an initial SVL of 8 mm or less (Fig. 1). Figure 2 illustrates the effect of the treatment variables on the number of tadpoles surviving each successive 24-hour census. Treatments containing *Gambusia* effected a decline in the tadpole population beyond the natural mortality rate. On average, 10% of the original 30 tadpoles in control treatments died after a 96-hour experimental trial, compared with 40% of tadpoles in open aquariums with *G. holbrooki*. In aquaria containing pondweed, 3% of tadpoles from the control treatments died compared to 17% of tadpoles exposed to fish predation for 96-hours. Comparison of the two graphs in Figure 2 suggests that the pondweed, *E. densa*, may influence *L. aurea* tadpole survival when *G. holbrooki* are present. Tadpoles in predator

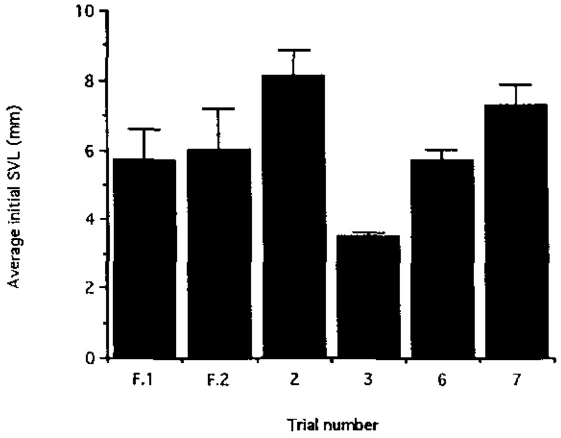
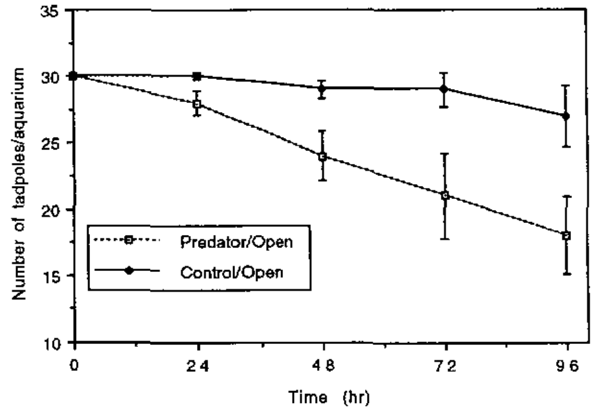


Fig. 1. Mean snout-vent length and standard error of the mean of pooled samples of *L. aurea* tadpoles, used for two field trials (F.1, F.2) and four laboratory trials (2, 3, 6, 7). Measurements made at the beginning of each experiment.

a) Open aquaria:



b) Aquaria containing the pondweed, Egeria densa:

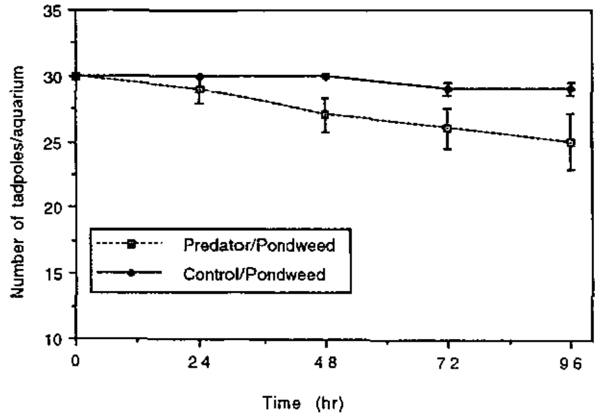


Fig. 2. Mean survivorship of *Litoria aurea* tadpoles in (a) open aquaria and (b) aquaria containing the pondweed *Egeria densa*. Aquaria from (a) and (b) were stocked with either 30 *L. aurea* (control) or with six *Gambusia holbrooki* and 30 *L. aurea* (predator treatment). Data are obtained from four pooled trials. Standard error bars indicate the variance about mean values.

Table 1. Statistical summary (two factor ANOVA) of the treatment variables (*Egeria densa*; Present/Absent and *Gambusia holbrooki*; Present/Absent) on the survival of *Litoria aurea* tadpoles under controlled laboratory conditions. Arcsine transformed data are from four trials with six replicates of each treatment.

Response variable	Source of variation	*d.f.*	F ratio	Probability
	24 hours $n = 24$			
Tadpole survival	*E. densa*	1	2.00	0.175
	G. holbrooki	1	7.56	0.014*
	E. densa × *G. holbrooki*	1	0.059	0.811
	Trial	3	3.08	0.055
	48 hours $n = 24$			
Tadpole survival	*E. densa*	1	1.92	0.183
	G. holbrooki	1	22.6	0.000**
	E. densa × *G. holbrooki*	1	0.153	0.700
	Trial	3	3.40	0.042*
	72 hours $n = 24$			
Tadpole survival	*E. densa*	1	3.81	0.068
	G. holbrooki	1	9.12	0.008*
	E. densa × *G. holbrooki*	1	1.01	0.329
	Trial	3	5.17	0.010**
	96 hours $n = 24$			
Tadpole survival	*E. densa*	1	6.24	0.023*
	G. holbrooki	1	26.7	0.000**
	E. densa × *G. holbrooki*	1	1.31	0.268
	Trial	3	6.56	0.004**

* = $P < 0.05$ ** = $P < 0.01$

treatments containing the buoyant pondweed appear to be preyed upon to a lesser degree than similarly placed tadpoles in open aquaria with *Gambusia*. However, ANOVA shows that the presence of *E. densa* had a significant effect upon tadpole survival only after 72-hours (Table 1).

Despite the reduced number of treatment replicates, the presence of the vertebrate predator, *G. holbrooki,* had a marked effect upon the survival of 30 *L. aurea* tadpoles. Analysis of both the field ($P < 0.031$ for all censuses) and laboratory trials (Table 1) revealed significant differences between control and predator treatments. At both locations, the six fish significantly reduced the number of tadpoles surviving daily predation within the first 24-hour census, and at every census that followed.

Tadpole survivorship was compared between trials. The number of *L. aurea* tadpoles censused after 96-hours in each of the field trials did not significantly differ ($F_{1,9} = 2.62$, $P = 0.149$) nor was there an effect of pond site ($F_{2,9} = 0.62$, $P = 0.564$). However, comparisons of tadpole survivorship between respective laboratory trials revealed significant differences at each census (Table 1). Differences may be linked to the range of body sizes used in laboratory trials (Fig. 1), although other effects, including a poor predatory response in the open predator treatments in trial 2 may have influenced the data.

Behavioural observations of laboratory trials, made before each census, revealed differences between tadpoles in control and predator treatments. In the presence of predators, most tadpoles restricted their movements and were not readily observed in the middle depths of the aquaria. Control tadpoles, by contrast, regularly swam across exposed areas and used all levels of the 21 cm deep water column.

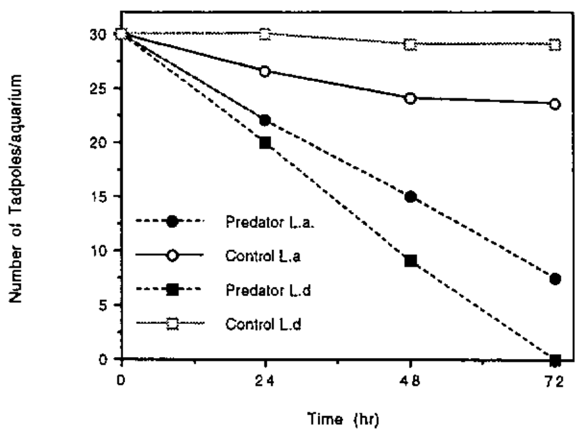
If disturbed by shadow, sound or motion, tadpoles responded by swimming away or diving down to the substrate. Smaller tadpoles (<5 mm SVL) were well concealed upon the substrate amongst large pebbles, particularly when their bodies were a light yellow colour. Tadpoles grouped between the aerator and aquarium wall, whereas individuals would occupy various regions of the floating pondweed.

Litoria dentata *Tadpoles*

The *Litoria dentata* trial used small tadpoles (SVL: 3.7 mm ± 0.06 s.e., $n = 240$). One aquarium containing fish and tadpoles (no pondweed) was contaminated, resulting in the death of all animals. To maintain control and predator treatment pairs within a trial, this aquarium and one control treatment (tadpoles only), selected at random were excluded from statistical analysis.

G. holbrooki eat *L. dentata.* After three days no tadpoles remained in the "open" aquarium, and

a. No pondweed



b. Pondweed present

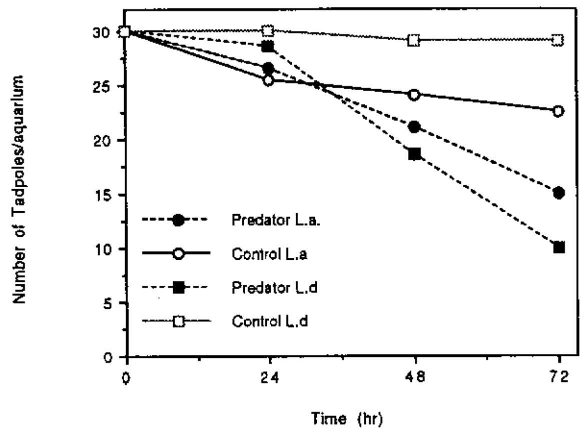


Fig. 3. Mean survivorship of 30 *Litoria aurea* tadpoles ("L.a") (SVL: 3.5 mm ± 0.13 s.e., n = 240) and 30 *Litoria dentata* tadpoles ("L.d") (SVL: 3.7 mm ± 0.06 s.e., n = 240) over a 72-hour sampling period in (a) open aquaria, and (b) aquaria containing the pondweed *Egeria densa*. Aquaria from (a) and (b) were stocked with either 30 tadpoles (control) or with six *Gambusia holbrooki* and 30 tadpoles (predator treatment). Data are obtained from two independent trials.

the other two predator treatments held less than 20 of the original 30 *L. dentata* sampled (Fig. 3). Similarly-sized *L. aurea* from trial 3 (SVL: 3.5 mm ± 0.13 s.e., n = 240; Fig. 2) are compared to the *L. dentata* trial in Figure 3.

More of the *L. aurea* tadpoles died than did *L. dentata* tadpoles in the control treatments. The age of each species may have influenced this difference, as the *L. aurea* tadpoles were five days old and *L. dentata,* six weeks old at the time of these trials.

Similar to *L. aurea*, the *L. dentata* population used in experiments declined over the period of study and attack(s) by *G. holbrooki* significantly reduced the *L. dentata* population by the second census (48h: $F_{1,4} = 57.5$, P = 0.017; 72h: $F_{1,4} = 124$, P = 0.001). In fact no *L. dentata* remained in the open aquarium with *G. holbrooki* after 72-hours. By the final census, *E. densa* is strongly implicated as facilitating the survival of *L. dentata* exposed to fish predators ($F_{1,4} = 101$, P = 0.009).

DISCUSSION

Litoria aurea tadpoles have been shown to be highly susceptible to predation by the introduced fish, *G. holbrooki* under controlled experimental conditions. In every treatment containing *G. holbrooki*, whether aquaria or cages, the number of *L. aurea* had significantly declined at each 24-hour interval sampled. In the single experiment using *L. dentata* tadpoles, exposure to *G. holbrooki* also significantly affected the survivorship of this species' tadpoles. A similar outcome has been found for the Australian frog species, *Limnodynastes peroni, Crinia signifera* (Webb 1994), *Lim. tasmaniensis, Lit. lesueuri* and *Lit. dentata* (Harris 1995).

The damselfly larvae which affected three of the laboratory trials are sit-and-wait predators (Caldwell *et al.* 1980), and were most likely present as eggs in the pondweed (Child 1968; Williams 1980) which hatched whilst in the aquariums.

The frequency and outcome of a predatory encounter may be mediated by a number of predator and prey attributes. The relative body sizes of predator and prey will act to partition the relationship by those prey too large or small enough to eat (Travis *et al.* 1985). Larval anurans are at their most vulnerable when small and recently hatched (Caldwell *et al.* 1980; Morin 1983; Travis *et al.* 1985). Tadpoles are also vulnerable during the transitional stage between aquatic and terrestrial existence (Duellman and Trueb 1986).

As a gape-limited predator, *Gambusia's* prey may fall within a definite size range, although Webb (1994) found that the body sizes of the *C. signifera* and *Lim. peroni* tadpoles did not significantly alter the level of predation by *G. holbrooki* after 24-hours. Webbs' 1994 study included tadpoles with "nibbled" tails as prey, in comparison to this study, which considered only deceased tadpoles to be prey. Williamson (1988) reported that prior to metamorphosis in a field population of *C. signifera*, over 90% of the tadpoles had damaged tails, which implies that predatory strikes on tadpoles are not uncommon (Richards and Bull 1990) and are not necessarily fatal.

The behaviour of prey affects the outcome of a predator-prey encounter. Active prey may be more conspicuous to predators (Lawler 1989; Peterson *et al.* 1992). In the control treatment *L. aurea* tadpoles were active throughout the water column, whereas tadpoles used in predator treatments were predominantly immobile and appeared to restrict their presence to marginal areas of the aquaria; upon the gravel substrate and alongside the walls of the bins. The gravel substrate in the aquaria may not be representative of the refuge opportunities found in natural environments. Specifically, benthos is usually composed of fine-grained particulate matter or silt. Silt can effectively conceal tadpoles (Lawler 1989), especially when stirred by an animal fleeing from attack. In the absence of detritus (leaf litter and other decaying matter), usual to aquatic environments, some cover was provided by lettuce fragments. The smallest tadpoles (e.g., trial 3) sheltered in the lee of stones, whereas larger tadpoles were observed in shallow depressions.

The presence of aquatic vegetation, modelled by *E. densa*, contributed significantly to *L. aurea's* survivorship at the final (96-hour) census, whereas, *L. dentata's* survival was significantly improved after 72-hours. This indicates that aquatic vegetation does provide some protection for tadpoles escaping attacks by fish. However, with so few replicates of each treatment, further work is recommended to substantiate this conclusion.

Breeding populations of *G. holbrooki* occur in both natural and altered, even heavily polluted habitats (Lloyd *et al.* 1981). *L. aurea* is primarily a permanent water breeder (Harrison 1922; Courtice and Grigg 1975; Humphries 1979; Gillespie *et al.* 1994), and some breeding populations are known to occur in recently disturbed aquatic environments (e.g., Port Kembla, New South Wales). In environments where the two species co-occur, it is likely that *L. aurea* tadpoles will be preyed upon by *G. holbrooki*. A response to the presence of these predators in permanent water-bodies may be the preferential use of ephemeral waters for breeding by some *L. aurea*, as noted by Daly, Pyke and White (pers. comm.).

Temporary aquatic habitats have an advantage for amphibian larvae because many of the predators typically found in permanent waters may be present at small densities or not at all (Roth and Jackson 1987; Kats *et al.* 1988). The results of this study identifies *L. dentata's* susceptibility to predation by *G. holbrooki*. *L. dentata's* use of ephemeral waters for breeding (Cogger 1992) may partly explain why there is no current evidence of a decline in the distribution or abundance of this species.

In summary, the tadpoles used in the laboratory and field-based experiments provide quantitative evidence of *G. holbrooki's* ability to decrease the number of larval amphibians present in a controlled two species system. *L. dentata's* susceptiblity to *Gambusia*-induced mortality, even though it is not declining in natural environments illustrates the non-specific predatory behaviour of *G. holbrooki*. As a result of these findings, remnant *L. aurea* populations are expected to be susceptible to *Gambusia*-induced mortality, when *G. holbrooki* inhabits their breeding sites. Removal of this introduced fish predator from these habitats is recommended as an appropriate action for the conservation management of endangered populations of *L. aurea*.

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